EXPERIMENTS ON COÖRDINATION AND RIGHTING IN THE STARFISH.

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In another paper (Cole, '13) I have presented and discussed the results of a series of experiments on the direction of locomotion of the starfish, *Asterias forbesi*, with respect to morphological axes, in the absence of directive stimuli. The experiments described in the present note were incidental to the more complete series just mentioned. They were performed tentatively to test the feasibility of certain lines of investigation which suggested themselves in the course of the other work, but which I have been unable to prosecute further. While they are not extensive enough to serve as a basis for far-reaching conclusions, they nevertheless supplement to some extent the observations of others, and, it is believed, suggest certain lines of research which might be followed up with profit. All of the experiments here described were made in November, 1909, in the animal behavior laboratory of the department of zoölogy, Sheffield Scientific School of Yale University.

In the locomotion of the starfish it was found that the "unified impulse" was an important factor, and Jennings ('07) had previously determined the same to be true in the righting reactions of the West Coast starfish, *Asterias forreri*, which he studied. The establishing of a "unified impulse" toward performing a definite action, such as turning on certain rays, or crawling in a certain direction, implies, of course, coördination. Loeb ('00) in his book on the "Physiology of the Brain" lays stress on coordination in the starfish, though apparently merely as an inhibiting influence, which prevents the rays not helping in a given reaction from working against its consummation, rather than one which causes them to join actively in bringing it about, that is, by taking part in a "unified impulse" toward that end. In discussing, for example, an experiment which will be mentioned later, he says (p. 63): "The experiments seem to indicate that

in a normal starfish the stimulus produced by the pulling of two or three arms in the same direction has an inhibitory effect on the other arms." Again (p. 65), he explains the movement of a starfish in a direction away from a ray which has been stimulated by saying that "the feet of this arm are drawn in and the arm becomes inactive," and "therefore, according to the parallelogram of forces, a movement away from the point of stimulation will take place." While stimulation of an arm may cause temporary inactivity of the feet of that arm and this might aid in initiating movement in the opposite direction (Moore, '10), the careful observations of Jennings ('07, p. 97) seem, however, to show that this explanation is only partial. He remarks on this point: "It is possible that in some cases when one ray is stimulated locomotion takes place entirely with the other rays, but such cases are very rare; though I have watched carefully for this, I have never seen one. As a rule the walking away from the stimulated region is due, like the usual locomotion of the starfish, to the coöperation and coördination of the tube feet of all the rays . . . . The active tube feet of all the rays are pushed forward in the direction in which the starfish is going; their suckers attach themselves, and by the contraction of the tube feet . . . the starfish is carried forward, the action of all the tube feet aiding in this." My own observations agree in this respect with those of Jennings. It is therefore evident that in locomotion as in righting an impulse is established, by which the different parts act in more or less complete harmony toward the accomplishment of a certain result. It is generally assumed, and is undoubtedly true, that this unity of action is made possible by the mediation of the nervous system.

Section of Radial Nerves.

The question naturally arises, however, whether it is not possible that an impulse toward the accomplishment of a definite end might be established without nervous connection between the different parts of the organism, just as an earthworm continues its coördinated locomotor contractions after section of the ventral nerve cord, or indeed if the worm itself be cut entirely through and the halves united by thread (Friedländer, 1888).

Here the muscular pull of the forward part acts as the stimulus for contraction in the posterior piece. Loeb's experiment in this connection was negative. He cut the nerve ring of a starfish at two points, nearly opposite to each other, thus severing the nervous connection of certain arms with the others. He found that whereas "the normal starfish requires but a few minutes to turn over, . . . the specimen [operated upon as described] remained on its back the whole afternoon, although the arms were struggling constantly to right it" (Loeb, '00, p. 63). Romanes ('85, p. 296) had, however, previously obtained different results in his experiments on the common British starfish. He states that when animals with the radial nerves severed at the bases of the arms are inverted, "the power of effecting the righting manœuvre is seen to be gravely impaired, although eventually success is always achieved." My experiments on *Asterias forbesi* agree in this respect with those of Romanes.

Experiment 1. (Specimen No. 10 of earlier paper.)—In three preliminary trials this specimen required 6 minutes, 5 minutes and 6 minutes respectively for righting, and turned on arms *cd*,[1] *bc* and *cd* in the successive trials. An incision was now made at the base of each arm, thus severing the radial nerves (and of course the radial water canals as well) close to their origin from the circumoral ring. The specimen was again placed on its back in the water, and the various arms at once began to make individual and apparently random movements toward righting.[2] While most of the arms went through various activities, bending and twisting, attaching and pulling, only to let go again, arm *c* persisted only in bending up orally, and did not twist and attach. This resulted finally, at the end of 20 minutes, in its becoming bent over far enough to obtain a hold between *a* and *e*, as shown in Fig. 1*A*. Arms *b* and *d* were also thrown well over at the

[1] Following Jennings ('07) the arms are designated *a*, *b*, *c*, *d* and *e*, beginning at the ray to the right of the madreporite and going around clockwise (cf. Cole, '13, p. 2). Dr. R. T. Jackson has emphasized (*in litt.*) the desirabilty of students of animal behavior, as well as specialists, using for the starfish the nomenclature introduced by Lovèn for the ambulacral and inter-ambulcral areas of Echini. With this view I am in accord and should have adopted the method had it not been that my earlier paper necessitated so much direct comparison with that of Jennings, and a different nomenclature would have made such comparison difficult.

[2] If there is any shock from the operation, it is so slight as to be hardly noticeable.

same time, but were not attached. Soon these latter straightened out again and the attachment of *c* was loosened. Twenty minutes later *c* and *d* bent over together and succeeded in obtaining a hold between *b* and *a* (Fig. 1*B*). By their concerted effort they succeeded in pulling the body over, *e* crossed over *a* (Fig. 1*C*), and at the end of 44 minutes from the time it was placed on its back the starfish had completely righted itself, turning, as seen, on arms *a* and *b*. It now remained quiet for two or three minutes, and then began crawling with *b* in advance, the movement being, however, very slow, as if there were not complete coördination of all the arms.

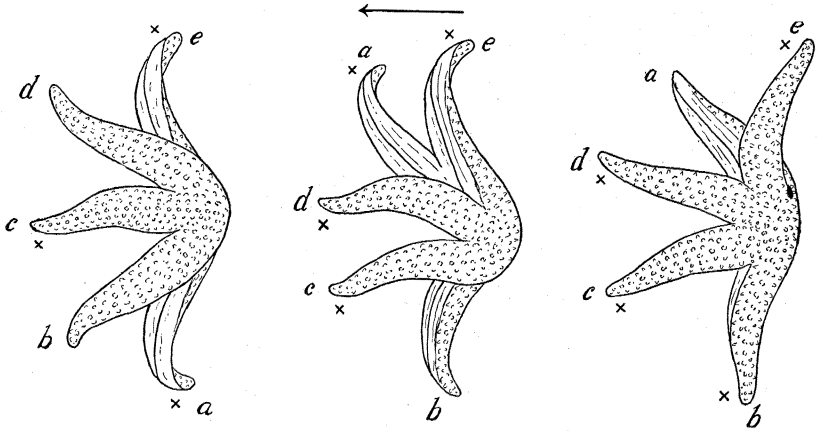

FIG. 1. Diagrams of righting movements of a starfish having the radial nerves severed at the bases of all the arms. Arms attached to substratum are indicated by ×. Arrow shows direction of turning.

Experiment 2. (Specimen No. 14.)—In eleven preliminary trials this animal righted itself in from one to five minutes, the average being 2.6 minutes. In ten of the trials it turned on arms $a + e$. An incision was now made on the oral side at the base of each arm, severing not only the radial nerve and water canal, but also the muscles and other internal organs, and leaving only the aboral arch of the external skeleton intact. It was now placed on its back in the water. It is unnecessary to give in detail the movements of the arms; it is sufficient to say that they at once began active but entirely uncoördinated movements.

Nevertheless, at the end of 56 minutes the animal had succeeded in righting itself, though arm *b* was still crossed over arm *a*. At the end of one hour, however, from the time it was placed on its back, it had straightened out completely. The turning was accomplished with arms *e* and *a*, although *c* swung over between them and really seemed most instrumental in pulling the animal over.

In both of these experiments the lack of coördination was very apparent, as mentioned by both Romanes and Loeb. Neither could it be determined that in either experiment a definite impulse toward turning in a given direction was established, as is normally the case. In fact, especially in the second experiment, it was noticed several times that as two or more arms happened at the moment to be working in concert, the righting could have been effected easily if another arm had but ceased its efforts in an opposite direction, to say nothing of helping in the same direction. The final turning appeared to be nothing but a chance occurrence when enough arms happened to be pulling in one direction to turn the specimen in spite of its other arms. Thus, although there resulted complete lack of coördination, as Loeb states is the case when the nerve connections are severed, the end result was nevertheless finally accomplished, apparently by accident. The pull of one arm on another does not seem, therefore, to be a sufficient stimulus to induce a definite coördination of the tube feet in the second arm.

The second specimen did not crawl after righting itself. It would be interesting to test whether by exerting a steady pull in one direction on such an "uncoördinated" specimen, a more or less unified impulse to crawl in that direction might not be induced, comparable to the crawling of the severed earthworm.[1] This experiment was not tried, but the lack of coördination shown in the righting would make it seem that a negative result might in all probability be expected.

[1] These experiments might be made even more comparable by severing the rays of the starfish completely from the disc and then sewing them in position again with thread.

Righting of Specimens with One or More Arms Removed.

The removal of one or more arms gives opportunity to test and observe the correlation in the remaining arms more closely. This study was not carried far, and a single example will suffice.

Experiment 3.—A starfish was tested a number of times and it was found that it turned regularly on arms $e + a$. Arms b and d were now severed completely at the base. If the animal now continued to turn on e and a, the only other arm concerned would be c, and it was expected that this would each time release as soon as coördination was established, allowing e and a to pull it over. It was proposed then to sever the nerve of c in order to destroy its coördination with the other arms, and to see if they combined would still be able to pull it over, or whether coördination might be reëstablished through the mechanical pull, without nervous connection. In the first two trials after the operation the specimen turned on e and a as expected (Fig. 2), but in the third trial c failed to coördinate properly and finally it with a pulled over e, which was doubled under until these arms had crawled far enough to enable it to straighten out.

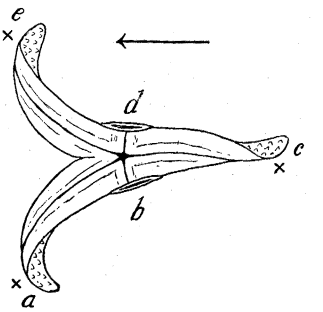

FIG. 2. Diagram of righting of a starfish with arms b and d removed. Nerves of other arms intact.

This experiment is not mentioned so much for the result obtained as to illustrate a possible method of studying coördination, impulses, and the relative use of the different arms in the starfish. It is important that the behavior of each specimen should be studied carefully in the normal condition before the operation is made.

Behavior of Completely Severed Arms.

Romanes ('85, p. 294) found that "single rays detached from the organism crawl as fast and in as determinate a direction as do the entire animals," and that "when inverted, separated rays right themselves as quickly as do the unmutilated organisms."

The question naturally arises, however, in the light of Jennings' observations that there is commonly a preference for the use of certain rays in righting, whether these same rays will be the first to turn if all are detached and inverted, and whether they will twist in the same direction as when helping to right the entire starfish. Will subsequent locomotion also be in the direction with respect to each of the arms that it would have been if the arms were attached?

The detached arms have two principal methods of righting themselves when inverted. The first is to curl up orally until they topple over one way or the other, when the tube feet attach and quickly right the arm. The other method is for the tip of the arm to twist until the tube feet can attach. They then start to crawl and the remainder of the arm is soon pulled over much after the manner in which a flatworm rights itself (Pearl, '03, p. 673). A sufficient series of experiments was not performed to answer the questions propounded above, the results so far as obtained being somewhat contradictory. More extended experiments, however, would probably lead to more definite results.

CONCLUSIONS.

As stated, the experiments mentioned above were rather incidental to other experiments on the starfish already reported (Cole, '13) and preliminary to others which it was hoped to continue. They are reported now not so much for the value of the results obtained as in the hope that they may stimulate further work along the same line. They do, however, seem to demonstrate, in so far as they go, the failure of the establishment of coördination or "unified impulses" in the starfish by direct pull of one part upon another when the nervous connection between these parts has been severed.

LITERATURE CITED.

Cole, L. J.

'13 Direction of Locomotion of the Starfish (*Asterias forbesi*). Journ. Exper. Zoöl., Vol. 14, No. 1, pp. 1–32.

Friedländer, B.

'88 Ueber das Kriechen der Regenwürmer. Biol. Centralblatt, Bd. 8, Nr. 12, pp. 363–366.

Jennings, H. S.

'07 Behavior of the Starfish, *Asterias forreri* de Loriol. Univ. Calif. Publ., Zool., Vol. 4, No. 2, pp. 53–185.

Loeb, J.

'00 Comparative Physiology of the Brain and Comparative Psychology. New York, G. P. Putnam's Sons, xii+309 pp.

Moore, A. R.

'10 On the Righting Movements of the Starfish. BIOL. BULL., Vol. 19, No. 4, pp. 235–239.

Pearl, R.

'03 The Movements and Reactions of Fresh-water Planarians: a Study in Animal Behaviour. Quart. Journ. Micr. Sci., Vol. 46, part 4, pp. 509–714.

Romanes, G. J.

'85 Jellyfish, Starfish, and Sea Urchins: Being a Research on Primitive Nervous Systems. Internat. Sci. Series, London, vii+323 pp.

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